Systematics of the Scurriini (New Tribe) of the Northeastern Pacific Ocean (Patellogastropoda: Lottiidae)

by

DAVID R. LINDBERG

Museum of Paleontology, University of California, Berkeley, California 94720, U.S.A.

Abstract. **Scurriini**, a new tribe of the subfamily Lottiinae Gary, 1840, is proposed for the lottiids of the Peruvian molluscan province in the southeastern Pacific (*Scurria* Gray, 1847, species) and *Notoacmea insessa* (Hinds, 1842) of the Californian and Oregonian molluscan provinces in the northeastern Pacific. **Discurria** new genus is proposed for *N. insessa* and the new, early Pleistocene species **Discurria radiata** from southern California. Recognition of the relationship between the genera *Scurria* and **Discurria** provides another example of a taxon shared by these two disjunct nearshore marine regions. The pattern of fossil and Holocene distributions of *Scurria* and *Lottia* Sowerby, 1834, in the eastern Pacific Ocean and Caribbean Sea suggests that migration and later radiations in the family Lottiidae have proceeded from south to north. This direction is unlike that of many other northeastern Pacific molluscan taxa that appear to have originated in the northwestern Pacific and migrated into the northeastern Pacific (west to east).

INTRODUCTION

Discontinuous spatial distributions of marine organisms are striking and important features in historical biogeography. Divisions in the distributions of nearshore marine molluscan taxa usually reflect prominent geological features or areas of geologically recent perturbations (*e.g.*, the Isthmus of Panama between the tropical eastern Pacific and the Caribbean Sea and the Wisconsian Glacial Period prohibiting exchange between the North Pacific and North Atlantic respectively).

While the absolute time of the event that divided a taxon can be used to estimate evolutionary or migratory rates, the pattern that emerges from any analysis is, to a large extent, dependent on the recognition of phylogenetic relationships between members of the fragmented fauna and flora (NELSON & PLATNICK, 1981; WILEY, 1981). When a clade has been divided relatively recently, the subclades tend to be more similar at lower taxonomic levels (*e.g.*, subspecies, species, subgenera) than clades that were separated earlier. For example, 92 species in 48 shared genera (about 2:1) occur in both the North Pacific Ocean and North Atlantic Ocean, separated by the Pleistocene glaciations of Arctic Canada during the last 0.150 Myr (data from DURHAM & MacNEIL, 1967:330), while only 56 species in 205 shared genera (about 1:4) are in common between the tropical eastern Pacific and Caribbean, separated by tectonic activity in Central America during the last 3.5 Myr (data from VERMEIJ, 1978:269).

The best documented cases of discontinuous distributions of marine molluscan taxa often involve east–west divisions (DURHAM & MacNEIL, 1967; VERMEIJ, 1978:242). However, one of the most intriguing discontinuous distributions occurs north to south—between the Californian and Peruvian molluscan provinces along the eastern Pacific margin.

The faunal and floral similarities between the Pacific coasts of temperate North and South America have been well documented in the terrestrial realm (CONSTANCE, 1963; RAVEN, 1963); GARTH (1957), MARINCOVICH (1973), WHITE (1986) and others have pointed out relationships between taxa in the nearshore marine habitats. In a study of the marine mollusks of Iquique, Chile, MARINCOVICH (1973) concluded that 49 intertidal genera out of a possible 68 (72%) were common to the Chilean and Californian provinces. However, Marincovich, like Garth before him, pointed out that further resolution of the pattern would require a better knowledge of the systematics of the faunas. This paper is a contribution towards that goal. Systematics follow LINDBERG (1986b); see also Table 1.

Table 1

Classification of northeastern Pacific Lottiidae.

Classification	Nomenclatural discussion
LOTTIIDAE Gray, 1840	LINDBERG, 1986b
PATELLOIDINAE Chapman & Gabriel, 1923	OLIVER, 1926; LINDBERG & VERMEIJ, 1985; LINDBERG & HICKMAN, 1986
LOTTIINAE Gray, 1840	herein
Lottiini Lindberg, new tribe	herein
Lottia Sowerby, 1834	LINDBERG, 1986b
Tectura Gray, 1940	LINDBERG, 1986b
Scurriini Lindberg, new tribe	THIEM, 1917; herein
Scurria Gray, 1834	McLEAN, 1973; CHRISTIAENS, 1975b
Discurria Lindberg, new genus	herein

SYSTEMATICS

Order Patellogastropoda Lindberg, 1986a

Superfamily Acmaeacea Forbes, 1850

Family LOTTIIDAE Gray, 1840

Shell composed of four to six shell layers. Innermost layer radial and/or complex crossed-lamellar followed by myostracum, optional radial crossed-lamellar layer, concentric crossed-lamellar layer, and prismatic layer(s). Radula three pairs of lateral teeth, marginal teeth two pairs, one pair, or lacking. Single gill in nuchal cavity typically present, but may be absent. Secondary gill in mantle groove present in some taxa.
Cretaceous to Holocene.

Subfamily LOTTIINAE Gray, 1840

Outer prismatic layer of shell consists of two layers; ventral portion fibrous prismatic, dorsal surface complex or simple prismatic. Marginal teeth one pair or lacking. Single gill in nuchal cavity present, and secondary gill in mantle groove present in some taxa.
Pliocene to Holocene.

Lottiini Lindberg, new tribe

Prismatic layer predominately fibrous with thin, outer layer of simple prismatic structure. Marginal teeth one pair or lacking. Looping of intestine typically simple with fewer than 3 loops. Secondary gill in mantle groove uncommon.

Distribution: [In the] EASTERN PACIFIC: Alaska to Peru.

Age: Pliocene to Holocene.

Discussion: The *Lottiini* appear to be derived from the Scurriini by the conversion of the exterior complex prismatic layer to simple prismatic and the expansion of the fibrous prismatic shell layer (see discussion below).

Remarks: Two eastern Pacific genera are referred to this subfamily, *Lottia* Sowerby, 1834, and *Tectura* Gray, 1847. Members of this tribe predominate in the Aleutian, Oregonian, Californian, and Panamic molluscan provinces (60°N to 5°S).

Scurriini Lindberg, new tribe

"Scurriiden" THIEM, 1917:613.

Prismatic layer predominately complex prismatic with thin, inner layer of fibrous prismatic structure. Marginal teeth one pair or lacking. Looping of intestine moderately complex (<5 loops).

Distribution: EASTERN PACIFIC [Disjunct]: Alaska to southern Baja California; Peru to Chile.

Age: Pliocene to Holocene.

Discussion: The shell structure of members of the **Scurriini** appears to be intermediate between the shell structure of the subfamilies Patelloidinae Chapman & Gabriel, 1923, and Lottiinae. In the Patelloidinae the outer shell layer is a single, uniform prismatic layer. In the Lottiinae the exterior prismatic shell layer consists of two layers, an inner fibrous layer and an outer complex or simple prismatic layer. The fibrous layer in the **Lottiini** is typically thick (about 60% of the prismatic layer) whereas in the **Scurriini** it is the thinnest shell layer (less than 20% of the prismatic layer). The shell structure of the **Scurriini** appears to be derived from that of the Patelloidinae by the differentiation of a fibrous prismatic shell structure from the ventral portion of the outer complex prismatic layer.

Remarks: Two eastern Pacific genera are referred to this subfamily, *Scurria* Gray, 1847, in the southern hemisphere and *Discurria* new genus in the northern hemisphere. Members of the genus *Scurria* form a diverse patellogastropod fauna in the Peruvian molluscan province (5°40'S to 42°S) (MARINCOVICH, 1973). The new genus *Discurria* occurs between higher latitudes in the northern hemisphere (25°N to 60°N) and is monotypic in the Holocene of North America. Both genera have members that are associated with large intertidal kelps.

THIEM (1917) was the first to recognize the distinctness of the tribe **Scurriini**, and diagnosed the "Scurriiden" from the "Akmaeiden" primarily on gill and shell characters; he also documented shell structure differences. From his hierarchical arrangement and "Resultate für die Phylogenie" (translated and reproduced here as Table 2), it is clear that Thiem considered this taxon to represent a natural group at the familial level. He further divided the "Scurriiden" into two subfamily-level taxa, the "Scurriididen" and the "Scurriidinen," distinguishing them from one another by a suite of alimentary characters.

Thiem's nominal taxa "Scurriiden," "Scurriididen," and

"Scurriidinen" are vernacular names, and because they were published after 1900, the names cannot be latinized and recognized as dating from THIEM's (1917) publication [Article 11f (iii) (ICZN, 1985)]. In a review of the history of patellogastropod classification, CHRISTIAENS (1975a) referred to two of Thiem's three taxa as Scurriidae and Scurriinae; however, he did not use or discuss these names in his classification. Therefore, while Christiaens correctly latinized Thiem's names, he did not use them as valid names for taxa and provided no descriptions or definitions, and thus they remained unavailable [Article 11d (ii) (ICZN, 1985)].

Discurria Lindberg, new genus

Type species: *Patella insessa* Hinds, 1842.

Shell: Profile medium to high; apex positioned in anterior one-third of shell. Anterior slope straight to convex, posterior slope convex. Radial and concentric sculpture present, typically weak. Exterior color brown with or without radial markings.

Radula: Lateral teeth unicuspid. Third lateral teeth lateral to second lateral teeth. Marginal teeth lacking. Ventral plates complex with strong anterior processes.

Animal: Left gill present in nuchal cavity.

Distribution: NORTHEASTERN PACIFIC: Alaska to southern Baja California.

Age: Pliocene to Holocene.

Etymology: *di-* (dis) apart + *scurria* (scurra) jester['s hat?]

Remarks: Monotypic in the Holocene, typically associated with the marine laminarian alga *Egregia*. Habitats more generalized in the late Neogene, occurring on hard substrata.

Discurria insessa (Hinds)

(Figures 1–3)

Patella insessa HINDS, 1842:82; pl. 6, fig. 3.

Shell (Figure 1): Profile high; apex positioned in the anterior one-third of shell. Anterior slope straight; posterior and lateral slopes convex. Lateral edges of shell parallel. Sculpture of fine riblets and concentric growth lines. Apex dark brown, with or without white markings; remainder of shell glossy brown. Interior of shell brown. Outcrops of shell layers along interior margin pronounced. Length, 5–20 mm.

Radula (Figure 2): Lateral teeth approximately equal in height; second and third lateral teeth broader than first lateral teeth. First lateral teeth closely set at anterior edge of ribbon segment, pointed distally, medial edge convex, lateral edges concave. Second lateral teeth broad, with straight cutting edge and pointed cusp displaced laterally;

Table 2

Systematics of the Scurriidae *sensu* THIEM (1917).

English translation of "Resultate für die Systematik."
A. Left neck gill in the nuchal cavity and true gill with lappets under the mantle edge, interrupted above the head. Radular formula 1·3·0·3·1; oral fringe around mouth; shell muscle segments 10–13 .... Scurriiden
I. Posterior region of the intestinal coil with single loop of the small intestine .... Scurriididen   Referred species: *Scurria viridula* (Lamarck, 1819), *S. zebrina* (Lesson, 1830), *S. coffea* (Reeve, 1855) [=*S. parasitica* (Orbigny, 1841)], *S. scabra chilensis* Thiem, 1917 [=*S. variabilis* (Sowerby, 1839)].
II. Posterior region of the intestinal coil with many loops of the small intestine. Furthermore: pharynxial salivary glands large and between the intestinal tract. Lappets on mantle edge much more numerous (as many as 10 per cm), almost a true gill type .... Scurriidinen   Referred species: *S. scurra* (Lesson, 1830), *S. apicina chilensis* Thiem, 1917 [=*S. scurra*].

third lateral teeth not reduced, pointed distally, lateral edge concave, forming a lateral extension of tooth. Only the dorsal portions of the lateral teeth are heavily mineralized. Ventral plates subrectangular with broad, flat anterior processes. First lateral plates rectangular; second lateral plates with straight posterior edges and fused with laterally positioned third lateral plates. Third lateral plates semicircular in shape.

**Animal:** White except for brown pigmentation of dorsal mantle edge. Snout with encircling oral fringe.

Distribution: ALASKA: Wrangell (56°20′N) to MEXICO: Baja California; Bahia Magdalena (24°30′N) (McLEAN, 1966:108).

Age: Pliocene to Holocene.

Remarks: The lustrous exterior surface of ***Discurria insessa*** has been commented on by DALL (1871) and almost every subsequent student of northeastern Pacific limpets. This surface, composed of complex prismatic crystals, and the convex medial edges of the radular lateral teeth distinguish ***D. insessa*** from all other North American species; both of these characters serve to unite ***D. insessa*** with the South American *Scurria*.

    Discurria insessa has most recently been assigned to the genus *Notoacmea* in systematic accounts of the northeastern Pacific patellogastropod fauna (CARLTON & ROTH, 1975; McLEAN, 1978; ABBOTT & HADERLIE, 1980; LINDBERG, 1981b). However, as early as 1871 DALL had pointed out similarities between ***D. insessa*** and members of the genus *Scurria* including: (1) the coloration patterns of young shells, (2) the outer, brown shell layers, and (3) the exterior sculpture. MACCLINTOCK (1967) further commented on the similar shell structure and protoconch morphologies of
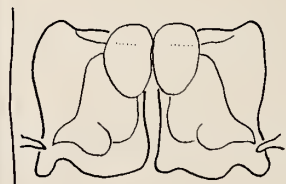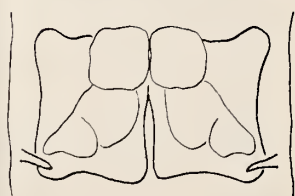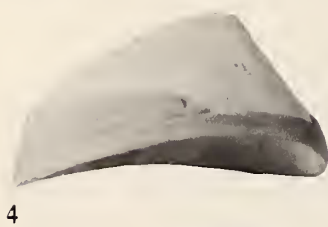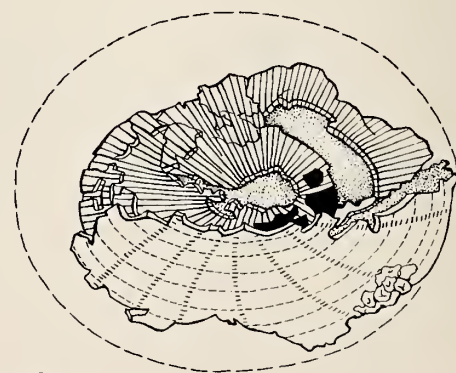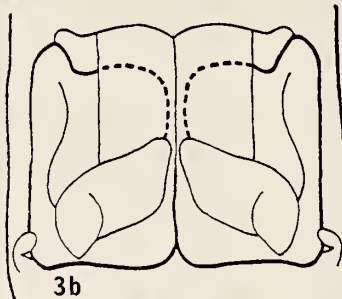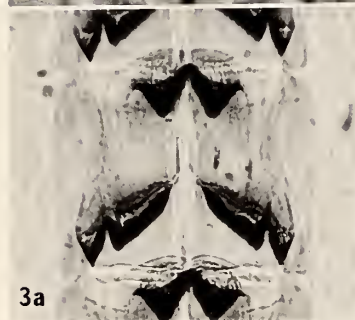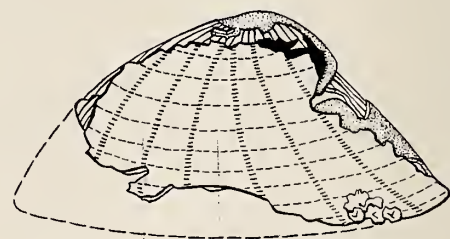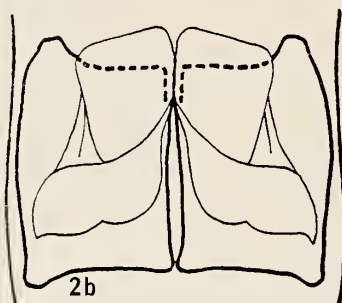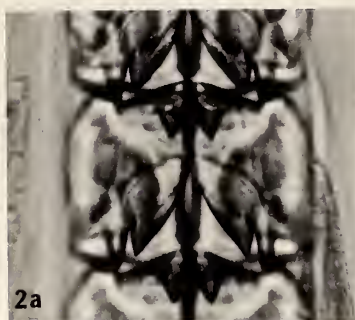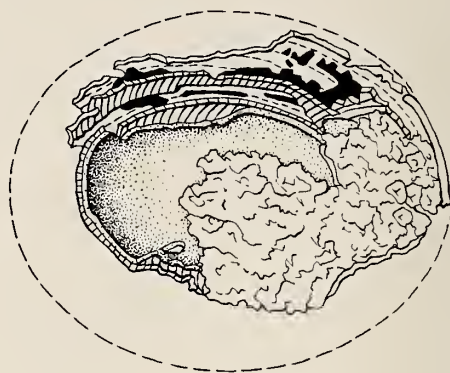
D. insessa and *Scurria scurra*, the type species of the genus *Scurria*. Neither worker commented on the shared characteristic radular lateral tooth shape (Figures 2, 3), and both gave too much phylogenetic significance to the presence of the secondary gill in *S. scurra*. It is now known that the secondary gill in members of the genus *Scurria* is variable in its development (McLEAN, 1973), and may be entirely lacking in some species. Moreover, secondary gills have arisen in many lottiid taxa and are poor indicators of phylogenetic relationships (LINDBERG & McLEAN, 1981; LINDBERG, 1983 and in press).

Discurria insessa is typically found on the stipes of the low intertidal laminarian alga *Egregia menziesii* (Turner) Areschoug, 1896. However, it also may occur on the shells of the mussel *Mytilus californianus* (Conrad, 1837) during the winter when the stipes of *Egregia* die back and are destroyed by winter surf. This has been observed along the rocky coast line of Santa Cruz County and on San Nicolas Island, Ventura County, California. At San Nicolas Island, what appeared to be the same individual limpets remained present on mussels (in fixed study quadrats) for up to four months before disappearing. It is not known whether these limpets subsequently returned to *Egregia* or died. Further study of this phenomenon is needed (also see Choat & Black, 1979).

The association of *Discurria insessa* with *Egregia* (and the resultant characteristic parallel lateral sides of the limpet) has not always been as fixed as it is in the Holocene. Some Pliocene and Pleistocene specimens of *D. insessa* have oval or highly irregular apertures that suggest that this species occurred on substrata other than *Egregia*, including rock and probably mussels (Figure 4).

Regardless of the apparent habitat plasticity seen in Neogene specimens of *Discurria insessa*, there is little doubt that its association with *Egregia* has been a strong selective force. The radular morphology of *D. insessa* suggests this association. The second lateral teeth with their broad, straight cutting edges are characteristic of patellogastropods that are associated with marine plants.

The recognition of a closer relationship between *Discurria insessa* and the Peruvian *Scurria* rather than with the North American Lottiinae necessitates reconsideration of ecological work that has been done with this species. For example, CHOAT & BLACK (1979) compared the life-history strategies of *D. insessa* and *Lottia digitalis* (Rathke, 1833). They reported that *D. insessa* has a higher growth rate, greater reproductive effort, and lower age of first reproduction than *L. digitalis*. From these findings, and because of the ephemeral habitat (the stipe of *Egregia* spp.) of *D. insessa*, CHOAT & BLACK (1979:43) concluded that "selective factors for the development of *A. insessa*'s life history may have been the life history characteristics of *Egregia*." Their scenario is consistent with the data, but the different phylogenetic histories of *D. insessa* and *L. digitalis* complicate this interpretation. Are the differences in life-history characteristics of these two species the result of selection operating in different types of environments as proposed by Choat & Black, or are they different merely because different lineages of patellogastropods have different life-history characteristics? It is not possible to resolve this question from available data, but comparisons of life-history characteristics of *D. insessa* with other *Scurria* species in the Peruvian province could help to resolve this question.

Between clade comparisons can present problems in interpretation of patellogastropod biological and ecological literature (Lindberg, in preparation). Sometimes the data from previous studies needs to be reanalyzed in light of phylogenetic relationships, and future studies should be designed to recognize and make comparisons within phylogenetic units (*i.e.*, clades) first so that trends, constraints, *etc.*, can be recognized before between clade comparisons or generalizations are made.

Discurria radiata Lindberg, new species

(Figures 5, 6)

Acmaea sp.: WATERFALL, 1929:checklist.

Shell (Figures 5, 6): Profile medium; apex position subcentral. Anterior slope concave, posterior slope convex. Lateral slopes straight. Reconstructed aperture oval.

←

Explanation of Figures 1 to 8

Figure 1. **Discurria** *insessa* Hinds, 1842. Holocene; Santa Cruz, Santa Cruz County, California. (UCMP Loc. E-756). Scale bar = 10 mm.

Figure 2. Radula of **Discurria** *insessa*. a. Lateral tooth morphology. b. Basal plate morphology.

Figure 3. Radula of *Scurria scurra* (Lesson, 1830). a. Lateral tooth morphology. b. Basal plate morphology.

Figure 4. **Discurria** *insessa* with irregular aperture. Pleistocene; San Nicolas Island, California; Terrace deposits (UCMP Loc. D-9614). Scale bar = 10 mm.

Figures 5 and 6. **Discurria** *radiata* new species. Holotype, UCMP Type No. 37530. Early Pleistocene; Saticoy, Ventura County, California; Saugus Formation (UCMP Loc. 7071). Figure 5: scale bar = 10 mm. Figure 6: solid light pattern = complex prismatic outer shell layer; solid dark = fibrous layer; hatched = concentric crossed-lamellar layer; stippled = radial crossed-lamellar layer; irregular, solid light pattern indicates the presence of matrix. Scale bar = 10 mm.

Figure 7. Radula of *Lottia mimica* Lindberg & McLean, 1981. Galápagos Islands. a. Lateral tooth morphology. b. Basal plate morphology.

Figure 8. Radula of *Lottia smithi* Lindberg & McLean, 1981. Galápagos Islands. a. Lateral tooth morphology. b. Basal plate morphology.

Sculpture of concentric growth lines. Exterior color tan with red-brown radial rays that gently curve from the apex to the shell margin. Interior of shell white.

Holotype dimensions: Length 12.0, width 8.6, height 6.2 mm.

Type locality: CALIFORNIA: Ventura County [Saticoy Quad]; Saugus Formation (34°18'N, 119°11'W). About 2 km [1.25 miles] N of mouth of unnamed canyon that lies 1.6 km [1 mile] E of Harmon Canyon, in creek bottom. Collector: L. N. Waterfall, December 1925 [Museum of Paleontology, University of California, Berkeley (UCMP) Loc. 7071].

Age: Early Pleistocene.

Type material: Holotype, UCMP Type No. 37530.

Etymology: *radius*- Latin noun, ray. Named for the red-brown radial rays that distinguish this species.

Discussion: Although based on a single specimen, *Discurria radiata* can be distinguished from other Pliocene, Pleistocene, and Holocene northeastern Pacific lottiid species by its shell structure, morphology and color pattern. Shell structure distinguishes *D. radiata* from all other Neogene and Holocene lottiids except *Discurria insessa*. Although the gross morphology of *D. radiata* resembles that of an oval *D. insessa*, the radiating red-brown rays are unique to *D. radiata*; the only markings found on *D. insessa* consist of variable white markings around the apex.

Although less than 75% of the total shell and 50% of the exterior surface remains on the holotype, there is no doubt that it is distinct from *Discurria insessa*. Neogene specimens of *D. insessa* are identical to Holocene specimens in gross morphology and color except for some Pleistocene specimens that have oval or irregular apertures (Figure 4). The conservative morphology of *D. insessa* through the Pleistocene corresponds to the narrow range of variation present in Holocene specimens. Little morphological variation is common in limpets that are associated with marine algae and angiosperms (LINDBERG, 1982 and unpublished data). Thus, the morphological stability of *D. insessa* over the last 1.5–2 million years suggests that it has been associated with *Egregia* spp. for this same period of time. In contrast, the straight sides of *D. radiata* suggest an oval aperture and there is no hint of parallel lateral edges. The reconstructed gross morphology of *D. radiata* is that of a rock-dwelling species, not a marine plant species (Figure 6).

The broken and exfoliated shell of the holotype exposes all four major shell layers of *Discurria radiata* (Figure 6). The only shell layer not visible to the unaided eye is the myostracum. The relative thickness of the various shell layers is similar to that of *D. insessa*.

Remarks: The Saugus Formation was considered by WATERFALL (1929) to be either Late Pliocene or Early Pleistocene in age, and the associated fauna warm-water in character. VALENTINE (1961) suggested that the Plio-Pleistocene boundary in the western Ventura Basin was in the Pico Formation, which underlies the Saugus Formation. Thus, the type locality of *Discurria radiata*, which is located in the western Ventura Basin, would be Early Pleistocene in age. Except for *D. radiata*, the fauna at UCMP Loc. 7071 (WATERFALL, 1929:checklist) is composed entirely of extant species that occur today along the central and southern California coast; there are no species that suggest that thermal conditions were any different from those of today. The fauna includes such rocky intertidal and shallow subtidal gastropod species as *Acanthina spirata* (Blainville, 1832), *Margarites lirulata* (Carpenter, 1864), and *Ocenebra foveolata* (Hinds, 1844); soft-bottom taxa, including the bivalves *Tresus nuttalli* (Conrad, 1837), *Macoma nasuta* (Conrad, 1837), *Modiolus rectus* (Conrad, 1837), and the gastropods *Polinices reclusianus* (Deshayes, 1839) and *Olivella biplicata* (Sowerby, 1825) are also present. VALENTINE (1961) concluded that the fossil assemblage at UCMP Loc. 7017 represented the *Tellina bodegensis-Forreria belcheri* community, which he considered to indicate a shallow, inner subtidal, chiefly sand-bottom habitat between 0 and 30 m in depth. *Discurria radiata* was probably transported into this depositional environment.

DISCUSSION

The recognition of the distinctness and taxonomic affinity of an incomplete patellogastropod limpet that was collected 60 yr ago was possible because original shell material was present. The importance of shell structure in patellogastropod systematics has already been demonstrated (MACCLINTOCK, 1963, 1967; LINDBERG, 1976, 1978, 1979, 1981a, 1983; LINDBERG & McLEAN, 1981; LINDBERG & HICKMAN, 1986). Moreover, shell-structure characters can be used for both fossil and Holocene specimens, and thus provide data for historical biogeography.

Californian and Peruvian Exchanges

The recognition of the relationship of *Discurria insessa* and *D. radiata* with the **Scurriini** of the Peruvian province provides another example of past faunal exchange between these two physically similar, but disjunct, molluscan provinces. Additional, previously unrecognized, northeastern Pacific rocky intertidal species that also appear to have immigrated from the southern hemisphere include: *Fissurella (Fissurella) volcano* Reeve, 1849, the single northeastern Pacific representative of a subgenus that is wholly restricted to the Peruvian province except for two outlying species (McLEAN, 1984b), and *Fissurellidea bimaculata* (Dall, 1871), the only northeastern Pacific member of a southern hemisphere group that is distributed from South America to South Africa (McLEAN, 1984a).

The genus *Discurria* first appears in the northeastern Pacific in the Pliocene of California at San Diego [UCMP Loc. 5092; San Diego Fm.] whereas *Fissurella s.s.* and

Fissurellidea first occur in the Early Pleistocene of southern California (GRANT & GALE, 1931). After these initial appearances, all three taxa quickly become common and abundant components in later Pleistocene faunas in southern and central California (GRANT & GALE, 1931; VALENTINE, 1961). It is also during the Pliocene that several northeastern Pacific taxa (*e.g., Chama* Linne, 1758; *Crenomytilus* Soot-Ryen, 1955; *Cryptomya* Conrad, 1848) first appear in the fossil record of northern Peru (T. DeVries, personal communication).

The above pattern of Holocene and fossil distributions and relationships suggests that during the Pliocene and Early Pleistocene the barriers (*e.g.,* temperature, current patterns) to faunal exchange between the temperate Californian and Peruvian provinces broke down more than once and taxa were able to move between the northern and southern temperate regions by crossing the intermediate tropical eastern Pacific. The movement of the Caribbean plate through the gap between North and South America (SYKES *et al.,* 1983), and the subsequent regional perturbations of temperature and currents in the marine environment (KEIGWIN, 1978, 1982) undoubtedly contributed to a changing regional setting across which the faunal exchanges were made.

Scurriini and the Evolution of the Lottiidae

While reviewing THIEM's (1917) monograph on the **Scurriini**, I realized that the endemic *Lottia* of the Galápagos Islands combine characters of both the **Scurriini** and the **Lottiini**. These endemic limpets have secondary gills with morphology similar to those in some members of the genus *Scurria,* but their shell structure is identical to that of *Lottia* species. Because secondary gills have arisen several times in different clades in the family Lottiidae (LINDBERG, in press), the presence of a secondary gill alone is not strong evidence for considering these species to be more closely related to the **Scurriini** than to the **Lottiini**. However, the lateral tooth morphology of the endemic Galápagos species (Figures 7, 8) has previously been seen only in members of the **Scurriini** (Figures 2, 3), and therefore, the Galápagos species may be more closely related to the **Scurriini** than previously thought.

The Galápagos endemics have characters that would place them in an intermediate position between the genera *Scurria* and *Lottia,* and they are known only from the Galápagos Islands, which places them directly between the centers of greatest diversity of both genera. If they are ancestral to **Lottiini**, their restriction to the Galápagos Islands, which have a depauperate Holocene patellogastropod fauna (LINDBERG & MCLEAN, 1981), would mean that the ancestral group survived in one of the only rocky intertidal faunas in the eastern Pacific Ocean without *Lottia* and *Tectura* species. Alternatively, they could represent a separate derivation from a different *Scurria* species.

The presence of the most primitive genus (*Scurria*) in the Peruvian province, the presence of possible intermediate species in the tropical eastern Pacific at the Galápagos Islands, and the derived genera *Lottia* and *Tectura* in the tropical eastern Pacific, Caribbean, and northeastern Pacific suggest that the direction of migration and later radiations of the Lottiinae may have been from south to north. This is in contrast to the common pattern of other molluscan groups that shows taxa originating in the northwestern Pacific and migrating into the eastern Pacific (MacNeil, 1965; Marincovich, 1984a, b).

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